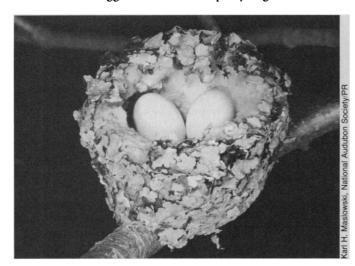
Egg Laying Is for the Birds

There are many notable things about birds, but one of the more remarkable is that all 9000 or so extant species practice the same mode of reproduction: they lay eggs. With the exception of the small and primitive class Agnatha, which includes the lampreys and hagfish, no other vertebrate class is so committed to egg laying as opposed to live births. Producing live young is clearly a reasonable reproductive strategy, as judged by the fact that it has arisen on at least 118 independent occasions among vertebrates, 93 of which are to be found among reptiles. So why have birds not joined the viviparity club?

"The literature is replete with statements to the effect that all birds lay eggs because as a group they are 'unable' to achieve viviparity," comment Daniel Blackburn of Vanderbilt University and Howard Evans of Cornell University. "The obvious alternative—that egg retention and viviparity might confer



From the smallest . . . a ruby-throated hummingbird nest, with 0.5-gram eggs

no net benefits on birds—is seldom considered." In other words, there is a widespread but usually unstated belief that what mammals do is in some way biologically superior, and that other vertebrates would be like mammals if they could be. Blackburn and Evans would like to encourage biologists to consider the alternative possibility, that in laying eggs and caring for hatchlings, birds achieve through their reproductive strategy whatever benefits mammals achieve through viviparity.

Some of the suggestions that have been advanced to show that birds are "unable" to evolve viviparity include the demands of flight, the unique structure of the egg, the mode of sex determination, immunological barriers, and the special requirements of lung development. None of these putative constraints can be tested directly of course, but, say Blackburn and Evans, each leads to certain predictions that can be examined.

For instance, the flight constraint, which has been the most popular in the literature, implies, among other things, that viviparity and flight are incompatible. The existence of bats falsifies this prediction. In addition, one might expect live births to evolve in flightless birds, which so far has not been observed. Birds do fly around with one fully developed egg on board, and it might be predicted that the mass of this single egg approaches the animals' carrying capacity. This too is falsified, be-

cause the ratio of egg mass to body weight in flying birds is generally in the range 1.8% to 12.5% as compared to the figure for lipid deposits in small migrating birds, which can be as high as 47%. The argument that birds are unable to be viviparous because of the demands of flight appears not to be upheld.

Blackburn and Evans examine each of the most common putative constraints in this way, and find no convincing reason why any of them should be a direct barrier to live births in birds. So where to go from here? "The absence of live-bearing birds can best be understood in the context of the evolutionary transition to viviparity that has occurred in other vertebrate groups," suggest Blackburn and Evans. That transition is thought to have involved a trend toward longer and longer retention of eggs, leading eventually to full gestation. Nothing of the sort appears to be even mildly developed in birds, except to a small degree in parasitic cuckoos. "Thus, the question of why there are no viviparous birds becomes one of why there are no birds in which even moderate periods of egg retention and intrauterine development occur." Blackburn and Evans answer their own question, by showing that the benefits to be gained through egg retention are outweighed by the costs.

The reproductive pattern of birds is unique among vertebrates, involving as it does the production of a single egg at a time and the elaboration of extensive maternal and (usually) paternal care, which imparts many of the supposed benefits of live births and infant care. "None of these specializations is inherently incompatible with egg retention or viviparity," say Blackburn and Evans. "Rather, these specializations have greatly diminished the potential advantages of egg retention while magnifying the associated disadvantages, such as loss of fecundity, increased maternal mortality, and decreased paternal investment." And the fact that birds of all sizes and all habits follow the same pattern "may reflect the effectiveness of the avian alternatives to egg retention."

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ADDITIONAL READING

D. G. Blackburn and H. E. Evans, "Why are there no viviparous birds?" Am. Nat. 128, 165 (1986).



... to the largest, it is eggs all the way. The nest of a mute swan, one of the largest of flying birds. The largest bird's egg is the ostrich's, which weighs 1450 grams.

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